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SIBLICIDE IN SWALLOW-TAILED KITES

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ABSTRACT.—We studied the reproductive behavior of Swallow-tailed Kites (*Elanoides forficatus*) in northern Guatemala. Modal clutch size was two (range 1–2), but no nests succeeded in fledging more than one young. Eggs were laid at intervals of three to four days and hatched at intervals of three to five days. Second eggs weighed significantly less than first eggs. Second chicks either received no food or obtained so little that they did not grow. First chicks vigorously attacked their nestmates, and all second chicks died within five days of hatching. Food stress was not found to be a proximate cause of this behavior. Siblicide appears to be innate in this population of Swallow-tailed Kites, even though the northern subspecies does not exhibit this behavior. Swallow-tailed Kites are, in certain aspects, an anomaly among species within the order Falconiformes that exhibit obligate siblicide. *Received 26 March 1996, accepted 29 Sept. 1996.*

Siblicide is known to occur in numerous raptor species as well as in egrets (Mock 1985), gannets (Jarvis 1974), boobies (Drummond 1986, Anderson 1990), skuas (Procter 1975), pelicans (Cash and Evans 1986), kittiwakes (Braun and Hunt 1983), and other birds. Among raptors, this phenomenon is most common in eagles (Brown 1966, Edwards and Collopy 1983, Gargett 1993).

There are two subspecies of Swallow-tailed Kites, (*Elanoides forficatus*). *E. f. forficatus* migrates from South America to breed in the southeastern United States. Numerous breeding studies have been conducted on this northern subspecies (Snyder 1974, Meyer and Collopy 1990, Cely and Sorrow 1990). Modal clutch size is two, and as many as three young have been reared successfully; two young fledge frequently. A single case of apparent siblicide has been documented for this subspecies (Sutton 1955); the smaller of two young died in week four after being injured and kept from food by its larger nestmate. *E. f. yetapi* occurs in Middle and South America with northern populations being migratory. In Tikal National Park, Guatemala, near the northern edge of the range of this subspecies, Swallow-tailed Kites have never been known to raise more than one young, and two-egg clutches have not been reported previously. In 1990 and 1991, we undertook a study in Tikal in which we regularly climbed to nests to determine the number of eggs and young, and conducted all-day observations at several nests. The results of that study are presented here with particular reference to siblicide.

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STUDY AREA AND METHODS

Tikal National Park is in the Department of El Petén, in northern Guatemala (17° 13′N, 89°38′W), where the semi-deciduous, lowland forest is classified as part of the Tropical Dry Life Zone (Holdridge 1957). Average annual rainfall is approximately 1.4 m (Smithe 1966); the area experiences distinct wet and dry seasons, the latter being from January to June. The main Maya ruins around which the park was established are on a limestone hill that is the highest point (250 m) for a considerable distance. This hill supports a dense concentration of nest sites of this loosely colonial species, and the ruins provided vantage points from which we found and observed the kites' treetop nests. We observed nest-building and courtship activities and, once a female began to spend more than an hour in an incubating posture, we climbed to the nest to verify the clutch.

We visited each nest every second or third day until the clutch was completed and then again when we expected hatching to occur. In some cases we were able to climb all the way to the nest; otherwise, we used a small mirror fixed to a pole to examine nest contents. Where possible, we measured and weighed eggs (within two days of laying) and young (periodically after hatching). We compared the mass of first eggs and second eggs using the Mann-Whitney *U* test (Zar 1984). Values throughout are means ± standard deviations.

We observed certain nests, selected for visibility, every third day throughout the incubation and nestling periods. Observations began 30 min before sunrise and ended 30 min after sunset. We recorded behavior of adults and young and the number and type of prey delivered to nests.

RESULTS

Swallow-tailed Kites placed their nests in the tops of the tallest emergent or lone trees. Mean tree height was 32.6 ± 4.8 m and mean nest height was 30.3 ± 4.8 m ($N = 22$). Nests were made of dead branches and vines; the nest cup was formed using *Usnea* lichens and Spanish moss (*Tillandsia usneoides*). Eighteen nests were found prior to or during incubation (nine each year). Fifteen eventually contained two eggs each; three held one egg each, giving a mean clutch size of 1.83 eggs.

Eggs within a clutch were laid three to four days apart and incubation began after the first egg was laid. Mean incubation period was 31.5 ± 0.9 days ($N = 6$ eggs for which laying and hatching dates were verified by climbing). At nine nests (five in 1990, four in 1991), both eggs hatched, with hatching intervals of three to five days. At eight of these nine nests, the second chick died when between three and five days old. In the ninth nest, both chicks were taken by predators on day four of the second chick's life; this chick was clearly dying when the breeding attempt failed.

One nestling fledged successfully from six of the 18 nests, four in 1990 and two in 1991. Thus, 33% of nesting attempts were successful, and 0.33 young fledged per nesting attempt (i.e., nests with eggs laid; $N = 18$). During this study, 1.00 young fledged per successful nest ($N = 10$, including four additional 1991 nests found during the nestling period); numerous anecdotal observations in years prior to and after the study

agree with this figure. In all six of the successful nests we observed, it was the first egg that produced the successful fledgling. In one of the 18 nests found during incubation, the second egg survived after the first fell out of the nest. Until the eventual failure of this breeding attempt, the second egg represented the only chance for success at this nest.

Second eggs ($\bar{x}$ = 33.6 ± 3.4 g, N = 5) were significantly smaller than first eggs ($\bar{x}$ = 40.7 ± 2.1 g, N = 4; U = 20, P = 0.02). Two first chicks weighed on day two had body masses of 41 and 37 g. Two second chicks had day-two body masses of 22 and 25 g, when their respective nestmates had body masses of 68 g (day five) and 93 g (day six).

We were able to observe siblicidal behavior at eight of the nine nests in which two eggs hatched. We conducted all-day observations at seven of these nests. In all cases, the first-hatched chick (A-chick) was seen attacking its younger nestmate (B-chick). This began shortly after B-chicks hatched and continued intermittently until their death. Most frequently, A-chicks pummeled B-chicks with their bills, with blows directed toward the head and neck. In addition, A-chicks grabbed B-chicks with their bills, pulling with an up-and-sideways wrenching motion. This latter maneuver was often directed at the head and neck, but occasionally a wing or back was treated in this manner. There was no battle; the undersized second nestlings never fought back or displayed any effective defence.

Aggressive attacks came in bouts lasting from a few blows to approximately 30 minutes. This behavior occurred both when the chicks were alone and when one of the adults was present. Although it was difficult to observe, we believe that brooding by a parent prevented the continuance of these attacks. Adults did not, however, intervene to stop attacks. A-chicks attacked B-chicks both when food was present and when food was absent. In some cases, attacks continued in spite of prey deliveries. Thus, the presence of food did not seem to stimulate aggressive behavior in A-chicks. Begging by B-chicks appeared to stimulate aggression from their nestmates. A prone and silent B-chick was much less likely to be attacked than one that was upright and calling. Nonetheless, B-chicks continued raising themselves and vocalizing as long as strength permitted.

It is difficult to identify with certainty the cause of death of the younger nestlings. The blows inflicted by their siblings did not lacerate the skin but may have caused some internal bleeding. The continued attacks weakened B-chicks to the point where they could no longer raise themselves to receive food. Moreover, they received little or no food to begin with; since the aggression of their older nestmates often placed them in a subordinate position when a parent arrived with prey. If individual B-chicks managed to receive food, it did not result in weight gain. Death always

occurred while they were not yet mobile enough to move to the edge of the nest and while A-chicks were not yet strong enough to push or pull them to the edge. We do not believe any B-chicks died as a result of falling from the nest. We suspect that starvation, possibly combined with internal injuries, caused the death of younger chicks.

We watched the death of the B-chick at one nest, where the young hatched three days apart. Four days after the second chick hatched, its older sibling attacked it throughout the morning and early afternoon. At first, the B-chick continued to raise itself, and its peeping seemed to provoke further attacks. It received no food during the entire day and grew weaker as the day progressed. By nightfall, it had been some time since it had raised his head; we believed it to be dead. We arrived at the observation point early the next day. As soon as the female, who had spent the night on the nest, awoke, she began picking at and eating the dead young. After taking several bites, however, she flew from the nest with the carcass and let it fall through the canopy.

Our observations did not indicate that food shortage (or competition) is a proximate cause of siblicide in this population of kites. Sibling aggression was not triggered by prey deliveries, and siblicide occurred at an age at which the food required by the brood of two was a small fraction of the food requirements later in the nestling period (Gerhardt et al., unpubl. data). Aggression continued unabated even when the A-chick was apparently satiated and refused further food. Siblicide and the associated aggression occurred predictably and regularly in both nesting seasons in which we conducted this study, and no nests of this population have been known to fledge two young in many years of casual observations prior to and following our study.

Two other isolated observations bear recounting here. At one nest at which we conducted focal observations, the second egg failed to hatch. The single young at this nest was observed pummeling this egg just as other A-chicks pummelled their siblings. We do not suggest that this behavior caused the egg to fail. Rather, we feel that this observation illustrates the degree to which aggressive behavior toward a nestmate is innate in these birds. Another nest that we observed closely was much delayed relative to other nests (and, we believe, represented a renesting attempt). At this nest, siblicide took place (a seven-day-old nestling killed its four-day-old sibling) at a time when other pairs of kites were delivering prey to single chicks nearly ready to fledge (40+ days after hatching). That is, single young were receiving ten or more prey items (invertebrates and vertebrates) with a total biomass in excess of 70 grams (Gerhardt et al. unpubl. data). Thus, prey availability at the time of this siblicide was much more than sufficient to provision the two young at this late nest.

DISCUSSION

Detailed descriptions of the behavior of young have been published for only four species of siblicidal falconiforms. Swallow-tailed Kites in Tikal are similar to Black Eagles (*Aquila verreauxii*; Gargett 1993) and unlike Lesser Spotted Eagles (*A. pomarina*; Meyburg 1970) in that B-chicks apparently do not alter their behavior in response to aggression from their nestmates. As in the kites we observed, neither Black Eagle nor African Hawk Eagle (*Hieraaetus fasciatus*; Meyburg 1974) B-chicks flee from this persecution; Lesser Spotted Eagle chicks do. At no time in their short lives did second Swallow-tailed Kite chicks exhibit normal growth.

Edwards and Collopy (1983) defined siblicidal species as "obligate" when the phenomenon occurs invariably and as "facultative" when it occurs occasionally. Simmons (1988) defined "cainism" as siblicide in the absence of food shortage and considered it obligate if occurring in more than 90% of cases. In accordance with these definitions, the Tikal population of Swallow-tailed Kites exhibits obligate cainism. Moreover, the siblicide we witnessed is also obligate when considering Gargett's (1993) argument that the distinction is absolute rather than relative. She stated that in facultatively siblicidal species the competition is for food, and death of the second chick is incidental to the struggle. For the kites we studied, as in the Black Eagles she studied, the immediate objective of the A-chick appears to be the death of its nestmate.

Our research allows us to add Swallow-tailed Kites to the ranks of known siblicidal birds. This finding is of particular interest both because Swallow-tailed Kites are an anomaly among obligately siblicidal falconiforms and because they exhibit intraspecific variation in the nature of this life-history strategy.

Traits that this population of Swallow-tailed Kites shares with other siblicidal falconiform species include a tropical distribution, a maximum clutch size of two (Simmons 1988), a longer hatching interval, and a greater difference in egg and hatching mass (Edwards and Collopy 1983) than species that are facultatively siblicidal.

Swallow-tailed Kites differ in many respects, however, from other obligately siblicidal species within this order. Most are large; the next smallest obligately siblicidal falconiform is the Augur Buzzard (*Buteo augur*; Gargett 1970a), which at 1100 g (female mass) is more than twice as heavy as a Swallow-tailed Kite. Other species that exhibit obligate siblicide have a delayed acquisition of adult plumage (Simmons 1988). Swallow-tailed Kites apparently acquire Definitive Basic plumage at 14–16 months (Meyer 1995), but plumage acquisition of the race *yetapi* remains poorly studied.

Such size and plumage traits are associated with longevity. This fact is an important assumption of Simmon's (1988) theory that cainism results in selection for quality and competitive ability. That is, obligately siblicidal falconiform species tend to experience extremely high subadult mortality and intense competition for breeding sites. Another concept advanced is that such species tend to be the most solitary species (Gargett 1970b, 1993). Again, Swallow-tailed Kites do not fit these trends. Little is known of the subadult mortality of this species. They do not experience intense competition for breeding sites, however, since these birds are loosely colonial, excluding other conspecifics only from the immediate nest area. Far from being solitary, Swallow-tailed Kites forage, roost, and migrate in large groups, and assist one another in nest defense (Meyer 1995, pers. obs.). Other siblicidal bird species besides falconiforms are colonial to varying degrees (Mock 1985, Cash and Evans 1986, Anderson 1990).

Whereas the population we studied exhibits obligate siblicide, no similar siblicidal episodes have been reported for the northern subspecies. The single documented case of siblicide in Florida (Sutton 1955) was probably a food-related brood reduction that occurred within the fourth week after the victim hatched. Two and sometimes three young regularly fledge from nests of this subspecies. The intraspecific variation documented here may provide a fertile area for research of the evolution of this phenomenon. To date, however, there are insufficient data from either subspecies to compare hatching success or to apply the insurance-egg hypothesis (Dorward 1962) to this species. Nonetheless, our findings prove that this reproductive strategy is not confined (within falconiforms) to the large eagles and suggest that the evolution of this phenomenon can occur at the subspecific level.

Two lines of inquiry can be pursued regarding siblicide such as this. The first suite of questions concerns the inability of such birds to raise a second young. Setting aside, for the moment, the mechanisms by which this strategy evolved, the basic answer is that the optimal brood size is (or was in the evolutionary past) one. A number of hypotheses regarding resource limitations have been put forth to explain not only siblicide but also the general trend in the tropics toward lower clutch and brood sizes than in more temperate zones (Lack 1966). Our research does little to advance such hypotheses; that brood sizes are smaller in this population of kites than in the northern subspecies is in keeping with this trend. The reproductive strategy of the sympatric Plumbeous Kite (*Ictinia plumbea*) supports the notion that some resource limits optimal brood size to one. Among raptors breeding in our study area, Plumbeous Kites are most similar to Swallow-tailed Kites in size, migratory strategy, nest placement,

feeding behavior and prey (Vásquez et al. 1992, Gerhardt, unpubl. data). This species not only fledges a single young, but lays only one egg (Vásquez et al. 1992, Gerhardt, unpubl. data).

The prey-size hypothesis (Mock 1985) proposes that small prey delivered directly to young (and thus monopolizable) can serve as a proximate trigger for sibling aggression. Young Swallow-tailed Kites are fed such prey, but it is not clear that there is any difference in this regard between the siblicidal population in Tikal and the northern subspecies, which does not exhibit siblicide (Meyer 1995). Moreover, sibling aggression in this study appeared to be independent of prey deliveries. These facts do not weaken the prey-size hypothesis but rather relegate its applicability, for this species, to the evolutionary past.

For species such as Black Eagles (Gargett 1993) and these Swallow-tailed Kites, innate aggression toward nestmates appears to be at least part of the mechanism for the continuance of siblicide. If this is the case, then a B-chick should exhibit aggressive behavior in cases where its disadvantages have been reduced or negated, either naturally or through brood manipulation experiments. We neither conducted any such experiments nor had any natural nests in which this could be tested—all B-chicks in this study were at too great a disadvantage to display such behaviors.

The second basic question concerns why, if optimal brood size is one, parents bother to lay a second egg. We can only speculate that, as in several other obligately siblicidal species (e.g., eagles, boobies, pelicans, and penguins, Dorward 1962, Warham 1975, Mock 1985, Cash and Evans 1986, Anderson 1990), a small percentage of successful fledgings in this population of kites will come from second-laid eggs, and that those eggs act as "insurance" (Dorward 1962) against loss of an entire nesting attempt should the first egg fail to hatch or result in a weak or deformed young. The "cost" to Swallow-tailed Kites of laying a second egg is clearly small, since mass of the second egg is less than 8% of female body mass and since little or no time is spent feeding second young. A much larger sample size is necessary before we can even begin to assess the "benefit" by learning how frequently second eggs result in successful fledgings.

Our results suggest that siblicide is genetically fixed to a considerable extent in this population of Swallow-tailed Kites. Behavioral observations indicate that sibling aggression occurs independent of prey deliveries and apparent hunger levels. Moreover, we have documented that this population of kites shares numerous traits (long hatching interval, difference in egg and hatching mass, regular and predictable nestling behaviors and siblicide) with other obligately siblicidal species for which food shortage has not been shown to be a proximate trigger (O'Connor 1978, Stinson

1979, Mock 1985, Gargett 1993). These findings do little to advance our understanding of the exact mechanisms responsible for the evolution of this reproductive strategy. Nonetheless, the knowledge that this strategy is employed by a small, gregarious species that differs in many respects from other obligately siblicidal raptors may slightly redirect efforts to explain the evolution of this phenomenon within the falconiforms.

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